DISTRIBUTION, ABUNDANCE, SIZE AND FEEDING HABITS OF *BRIENOMYRUS BRACHYISTIUS* (GILL, 1862) (TELEOSTEI : MORMYRIDAE) IN A NIGERIAN RAINFOREST STREAM

by

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ABSTRACT. - *Brienomyrus brachyistius* (Gill, 1862) constitutes 64 % of the total number of all mormyrid species caught from the upper and middle reaches of Ikpa River in the rainforest zone of south-eastern Nigeria. It inhabites shallow marginal areas and swamp-pools with aquatic macrophytes. *B. brachyistius* feeds primarily on benthic invertebrates (with chironomid larvae predominating), algae, detritus and secondarily on zooplankton, miscellaneous invertebrates and mud/sand ; allochthonous invertebrates and macrophyte material are of incidental importance. The diet varies slightly with growth and season. Feeding activity is higher in the small-sized guild (< 10 cm TL) than large-sized guild (≥ 10 cm TL) ; it is intense at night but declines during the day and is higher in the dry season than during the rains. Seasonal fluctuations in hydrometeorological regimes (rainfall, water level, flow rate) are critical factors that affect the food and feeding habits of the fish ; flood has a depressive influence on food variety and feeding intensity.

RÉSUMÉ. - *Brienomyrus brachyistius* (Gill, 1862) constitue 64 % du nombre total de mormyridés capturés dans les parties supérieures et moyennes de la rivière Ikpa dans la forêt humide du sud-est nigérien. Cette espèce vit près des rives, dans des endroits peu profonds et dans des mares contenant des macrophytes aquatiques. *B. brachyistius* se nourrit principalement d'invertébrés benthiques (dans lesquels les larves de chironomidés sont prédominantes), d'algues, de détritus et, secondairement, de zooplancton, d'invertébrés divers et de sable ou de vase ; les invertébrés allochtones et les macrophytes sont d'importance mineure. Le régime alimentaire varie légèrement avec la croissance et la saison. La recherche de nourriture est plus active pour les petits individus (< 10 cm TL) que pour les grands (≥ 10 cm TL). Très intense la nuit, elle décroît pendant la journée et elle est plus importante pendant la saison sèche que pendant la saison des pluies. Les variations saisonnières du régime hydrométéorologique (pluie, niveau des eaux, vitesse du courant) sont des facteurs qui affectent la nourriture et les habitudes alimentaires du poisson. Les inondations ont une influence néfaste sur la diversité de la nourriture et sur l'intensité de la recherche de nourriture.

Key-words : Mormyridae, *Brienomyrus brachyistius*, Ikpa River, Nigeria, Ecology, Hydrometeorological regimes.

Brienomyrus brachyistius (Gill) is a common mormyrid with wide geographic distribution in fresh-water coastal drainages from Gambia to Zaire (Trewavas and Irvine, 1947 ; Trewavas, 1974 ; Gosse, 1986). Very little attention has hitherto been given to the biology and ecology of this species, apparently because of its small size which precludes its validity as a commercial species ; available literature includes brief accounts of its longitudinal distribution in Ogun River, Nigeria (Sydenham, 1977), habitat preference in rivers in northern Nigeria (Reed *et al.*, 1967), western Cameroon (Trewavas, 1974), Ouémé River basin, Benin Republic (Welcomme, 1979 ; 1985), Niger River (Welcomme, 1986) and food habits in Ouémé River system (Welcomme, 1979, 1985). The dearth of bioecological information on *B. brachyistius* provided impetus for the present study (April, 1986 - May, 1987 inclusive) on the population in Ikpa River, a tropical rainforest stream in Akwa-

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Ibom State, southeastern Nigeria. This involves *inter alia*, its spatial distribution, habitat preference, relative abundance, size, food and feeding habits.

Study area :

Ikpa River (Fig. 1) is a perennial tributary stream West of the lower reaches of the Cross River. It drains a catchment area of 516.5 km^2, 14,8 % (76.5 km^2) of which is liable to annual flooding. The entire length of the main channel (c. 53 km) lies at the interface of two different geological deposits : tertiary sedimentary rocks and cretaceous deposits (see geological map of Nigeria in Clausen, 1964). The stream is considerably shaded by overhanding canopy of riparian vegetation (mostly *Elaeis guineensis*, *Raphia hookeri* and *R. vinifera*). The littoral macrophytes are mainly *Nymphaea*, *Vossia* and *Crinium* species.

Climate of the area is typical of tropical rainforests ; it comprises dry (November-March) and wet (April-October) seasons. Climatological data from the University of Cross River State meteorological station (No. 0507.05B) at Uyo (Fig. 1) indicates that the dry season is characterized by prevalence of dry tropical continental winds from the Sahara desert and low mean monthly precipitation (3.5-13.6 cm) ; peak dry season occurs in December - February. The wet season is characterized by prevalence of moist tropical maritime winds from the Atlantic Ocean and high mean rainfall (23.0-39.2 cm) with a double maximum, in July and September ; an intermediate rainless spell of 7-21 days occurs in August. Annual rainfall is 258.1 cm, 82.6 % of which is received in the wet season. Hydrological observations during this study (King, unpublished) reveals that fluctuations in stream level and flow rate (current velocity) are determined by intensity of precipitation and contribution from runoff from the riparian zone ; these produce a cyclic hydrological regime typified by high water level and flow rate during the rains and *vice-versa* in the dry season.

Fish samples were collected at five stations (Fig. 1) : 1-2, 3-4 and 5 are on first, second and third order streams respectively as defined by Keuhne (1962). Stream size and depth increase from station 1 (mean width = 3.39 m ; mean depth = 0.33 m) to 5 (mean width = 78.40 m ; mean depth = 5.75 m). The substratum at each station is predominantly (> 70 %) fine sand.

MATERIALS AND METHODS

Fish sampling was conducted at each station with 5 unbaited conical-valved basket traps (each 80 cm long, 88 cm diameter of opening) similar to the one figured in Trewavas *et al.* (1972 p. 92). A month's sample consisted of catches on five consecutive days and nights. Traps were set in open water, vegetated areas, fringing swamps and in areas with different substrate - types ; those for night catches were set at dusk and examined at dawn and *vice-versa* for day catches. *B. brachyistius* caught were counted, measured (cm) (total length (TL) and standard length (SL)) and weighed (g), (wet weight (W_t)) after draining water from the buccal cavity and blot-drying ; they were preserved in 10 % formalin pending further examination. Other mormyrids caught in association with *B. brachyistius* were identified and counted.

Each randomly selected specimen of *B. brachyistius* was later dissected to remove the intestine which was unravelled and the length measured (cm) ; relative intestinal length (RIL) was calculated by expressing intestinal length as percentage of TL.

Other morphological attributes of the gut (mouth orientation, snout protrusibility, dentition, gape) related to trophic ecology were noted. The 'points volume' of food in the stomach (cf. Olatunde, 1978) was used to evaluate feeding activity based on the assumption that feeding intensity positively correlates with amount of food ingested. Each slit stomach was assigned a number of points proportional to its degree of fullness according to an arbitrary 0-20 scale ; thus, 0, 5, 10, 15 and 20 points were scored for empty, 1/4 full, 1/2 full, 3/4 full and full stomachs respectively ; mean feeding intensity (MFI) was calculated as mean points per stomach.

The contents of each stomach were placed in a petri-dish ; aggregates were dispersed with a small amount of water and subsamples taken for microscopic and macroscopic analyses of the composition. The dietaries were identified and the item occupying the greatest stomach volume was recorded as 'dominant content' and then all others were listed. Food-richness (N_f) was regarded as the number of food categories in the diet. The percentage relative frequency (RF) and dominance (RD) of each item were computed according to the formulae :

$$RF = \frac{fi}{\sum_{i=1}^{n} Fi} \times 100 \qquad RD = \frac{di}{\sum_{i=1}^{n} Di} \times 100$$

where f_i = frequency of item i ; F_i = frequency of the nth item (= sum of all f_i) ; di = frequency of item i as dominant dietary ; Di = frequency of the nth dominant item (= sum of all di). The RF and RD of all dietaries sum up to 100 % respectively. The 'integrated importance' of each item was estimated by a percentage index of food preponderance (IFP) calculated as the mean of % RF and % RD ; primary dietaries were considered as those with IFP ≥ 10 % while those with values from 1 to < 10 % were regarded as secondary ; items with IFP < 1 % were classified as incidental. The RF and RD methods are unweighted by the actual amounts of items in the stomachs but are responsive to the frequency of each as dominant and subsidiary content in relation to the frequencies of all other dominant and subsidiary dietaries respectively.

They are modifications of the methods used by Trewavas *et al.* (1972). The RF method over-emphasizes the importance of numerous small items such as unicellular algae while the RD method over-emphasizes the importance of large items such as macroinvertebrates. However, the use of IFP to establish overall food importance minimises the bias that could have accrued if results from the different analytic methods were independently interpreted.

Diet breadth which provides an indication of the degree of dietary specialization, was measured on IFP data by Shannon's diversity index (H') which was scaled such that one represented an even distribution and zero, a strongly skewed distribution (Odum, 1975). Intraspecific dietary overlap was calculated on IFP data using the similarity index, S (Moss and Eaton, 1966) :

$$S = \sum_{i=1}^{n} \min. (X_i, Y_i)$$

where Xi and Yi = proportions of each of the components of the series of nth item comprising the diets of X and Y. This index ranges from zero, for totally dissimilar dietary compositions to 100 %, for identical diets. Fish specimens were categorised into two size-guilds for the purpose of evaluating changes in food and

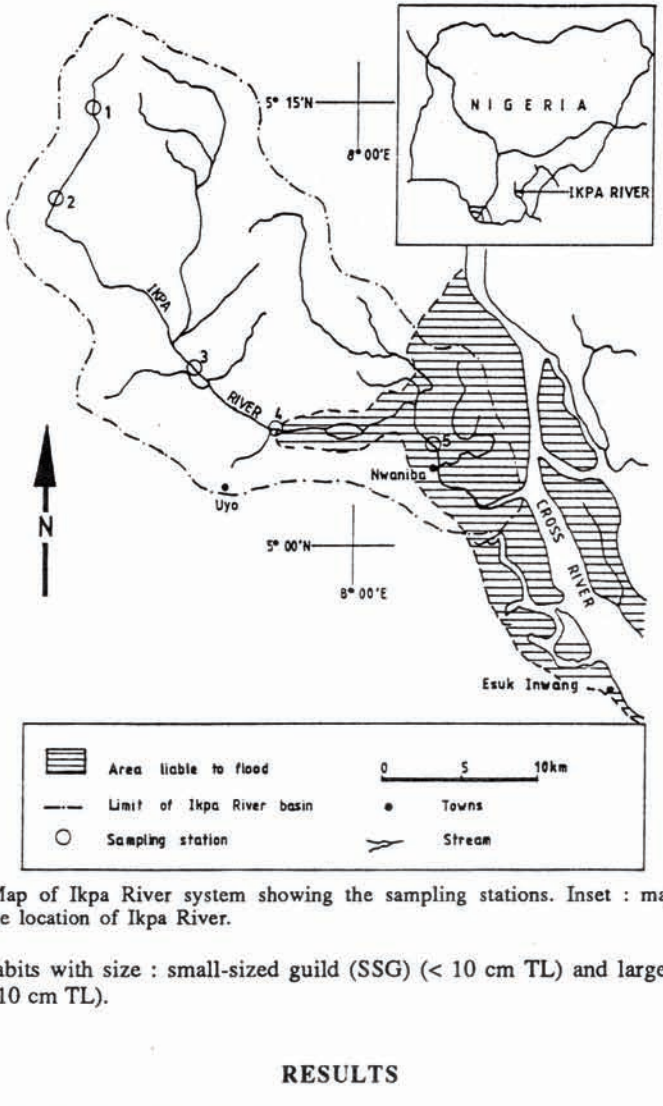

Fig. 1 : Map of Ikpa River system showing the sampling stations. Inset : map of Nigeria showing the location of Ikpa River.

feeding habits with size : small-sized guild (SSG) (< 10 cm TL) and large-sized guild (LSG) (≥ 10 cm TL).

RESULTS

Distribution and habitat

B. brachyistius was present only at stations 1-4 in the upper and middle reaches of the river. This contrasts with Sydenham's finding (1977) that this species is limited to the lower reaches of Ogun River. The occurence of *B. brachyistius* in catches throughout the year in Ikpa River indicates that it is a resident species ; it is an epibenthic fish, preferring quiet and gently-flowing stretches and muddy substratum or fine sand overlain with a layer of organic debris ; it tended to evade swift stretches of water and areas with coarse substrata, *B. brachyistius* was found most commonly in shallow marginal water amongst aquatic macrophytes and in swamp-pools. During the rains, it was rarely found in the main stream channel, the bulk of the collection coming from marginal vegetation, swamps and other sheltered areas ; this is probably a distributional strategy to evade the characteristic high water level and flow rate during this period. It may also be due to lateral movement of the fish into fringing swamps to breed. In the Niger River, it breeds in the adjacent floodplains (Welcomme, 1986). Most specimens of *B. brachyistius* came from night catches whereas < 5 % was caught during the day ; it was found in association with *Isichthys henryii* Gill, *Pollimyrus isidori* (Cuvier and Valenciennes), *Marcusenius abadii* Boulenger and *Gnathonenus petersii* (Günther).

In West Cameroon, *B. brachyistius* is found in streams with swift water under shelter of rocks and marginal vegetation (Trewavas, 1974) while in the main channel of the Ouémé River, it inhabits the bottom zone (Welcomme, 1979) as well as bank vegetation (Welcomme, 1985) ; in the main channel and floodplain pools of the Niger River, *B. brachyistius* inhabits fringing vegetation and prefers muddy substratum (Welcomme, 1986). These reports conform to the present finding on the habitat preference of *B. brachyistius* in Ikpa River.

Relative abundance

B. brachyistius was numerically the most abundant mormyrid in the river, constituting 64 % of the 1512 mormyrids caught. It was usually caught in numbers ranging from 1 to 10 per trap albeit Trewavas (1974) has noted its occurrence in aggregations of c. 20 fishes. *B. brachyistius* was the dominant mormyrid at all stations within its longitudinal range of occurrence. Spatial variation in relative abundance ranged between 48.6 and 93.8 % of all mormyrids per station. Of the 968 specimens of *B. brachyistius* sampled during this study, 33.3 % was caught during the rains and 66.7 % in the dry season. Its greater abundance during the dry season can most likely be attributed to the concentration of the fish in a smaller volume of water, thus increasing sampling efficiency. Reed *et al.* (1967) have noted that mormyrids of the genus *Marcusenius (B. brachyistius* formerly was placed in this genus) are usually most abundant at the onset of the dry season in northern Nigeria.

Size

Total length is used in this paper but can be converted to SL from the following linear relationship ($r = 0.995$, $P < 0.002$, $n = 32$) :

$$SL = 0.972242\ TL - 0.587425.$$

Since some workers use TL and others SL, knowledge of this relationship is useful for comparative purposes as it provides the basis for converting TL to SL and *vice-versa*. The smallest and largest individuals of *B. brachyistius* recorded measured 3.1 and 16 cm TL respectively. This species can however attain a size of up to 17.8 cm TL (Trewavas and Irvine, 1947). Fish of the LSG were caught only at stations 1 and 2 whilst those of the SSG were present in catches from all stations, suggesting that the latter was more widely distributed.

There was a significant correlation between TL and W_t ($r = 0.972$, $P < 0.002$, $n = 50$) of *B. brachyistius* ; an exponential relationship of the form :

$$W_t = 0.182059\ TL^{2.538406}$$

accounted for 94.6 % of the variation (r^2) in weight.

The value of the length exponent ($b = 2.538406$) in the length-weight regression which is less than the cubic value (3), indicates that increase in size is allometric ; this implies that the fish becomes less rotund as it grows in length (Anderson and Gutreuter, 1983).

Diet

Composition : The trophic spectrum of *B. brachyistius* (6-15 cm TL, $n = 129$) (Table I) indicates a high food-richness ($N_f = 28$). The IFP shows that it fed primarily on benthic invertebrates (56.6 %), algae (18.9 %) and detritus (12 %) and secondarily on zooplankton (2.4 %), miscellaneous invertebrates (1.1 %) and mud/sand (8.2 %); allochthonous invertebrates (0.4 %) and macrophyte material (0.4 %) were of incidental importance.

Of the benthic invertebrates ingested, chironomid larvae were most important (IFP = 36.9 %) while each of the others formed less than 7 % (IFP) of the diet. The preponderance of chironomid larvae in the diet of *B. brachyistius* is comparable to Hyslop's (1986) finding on ***Petrocephalus bovei*** (Valenciennes) and ***Marcusenius senegalensis*** (Steindachner) in floodplain pools of the Sokoto-Rima River basin, Nigeria. Nikolsky (1963) has commented on the considerable importance of chironomid larvae in the diets of fishes inhabiting stagnant or slow-flowing water.

The large proportion of this item in the diet of *B. brachyistius* in Ikpa River is thus a reflection of its habitat preference. Only small amounts of chironomid pupae, ephemeropteran nymphs, ostracods and *Arcella* were consumed as evidenced by their absence as dominant dietaries. The algae consumed were predominated by periphytic filamentous forms (IFP = 13.1 %) (*Spirogyra, Oscillatoria, Lyngbya)* ; planktonic colonial algae (*Volvox, Pandorina, Eudorina*) and euglenids (*Phacus, Euglena*) occurred in small amounts (IFP = 0.4 % respectively) in the stomachs ; diatoms (IFP = 2.6 %) (*Navicula, Nitzschia, Surirella, Pinnularia, Gomphonema, Amphora*) and desmids (IFP = 2.4 %) (*Closterium, Docidium, Plurotaenium, Cosmarium, Penium, Euastrum*) comprised mostly periphytic/epibenthic forms. Of the two forms of detrital particles ingested, coarse particulate organic matter (dark angiosperm tissues, comprising fragments of bark and decaying shed leaves of riparian macrophytes) was most important (IFP = 8.1 %) while fine particulate organic matter formed less than 4 % (IFP) of the diet. The predominance of coarse particulate organic matter is a reflection of its abundance in the stream.

The ecological significance of this item as main energy source in headwater streams has been discussed by Welcomme (1985).

The ingestion of allochthonous invertebrates that fall on the stream surface from overhanging vegetation indicates some degree of surface-feeding while mid-water feeding is evidenced by the consumption of phyto and zoo-plankton. Mud/sand found in the stomachs may have been inadvertently ingested during benthic foraging. This is supported by the fact that no stomach was found exclusively with mud/sand ; the presence of associated organic matter and epibenthic algae in the stomachs however, indicates that some nutritional benefit may accrue from the ingestion of mud/sand, although this is not comparable to that derived by deposit-feeders that subsist predominantly on mud/sand with associated organic matter, epipelic/episammic algae and microzoobenthos (Welcomme, 1979, 1985, 1986).

The wide variety of items in the diet of *B. brachyistius* demonstrates its high trophic flexibility. The adaptive significance of evolution of a broad trophic spectrum and ability to exploit the surface, mid-water, bottom and aufwuchs trophic niches is that it facilitates adequate utilization of available food ressources as well as enable the fish to easily switch from one food category to another in response to fluctuations in their abundance and availability. There are hitherto no detailed records of the diet of *B. brachyistius*. It is simply considered as an 'aufwuchs browser' (Welcomme, 1979) and 'micropredator' (Welcomme, 1985) in Oueme River basin. These generalizations are partly in consonance with the present finding in view of thelarge proportions of aufwuchs algae and minute invertebrates in the diet (Table I).

Variation with size : Diets of the two size-guilds of ***B. brachyistius*** are presented in Figure 2. Food-richness for the SSG (N_r = 25) was slightly higher than the value for the LSG (N_r = 22) ; these were positively correlated with changes in MFI with growth (Fig. 3), thus indicating that food-richness increases with feeding

Table I : The dietary composition of *B. brachyistius*. RF = relative frequency ; RD = relative dominance ; IFP = index of food preponderance.

Food items	% RF	% RD	% IFP
Algae			
Filamentous algae	11.2	15.1	13.1
Colonial algae	0.7	-	0.4
Unicellular algae : Diatoms	3.9	1.4	2.6
Desmids	1.4	3.4	2.4
Euglenids	0.7	-	0.4
Detritus			
Coarse particulate organic matter	12.7	3.4	8.1
Fine particulate organic matter	7.1	0.7	3.9
Benthic invertebrates			
Diptera : Chironomid larvae	19.8	54.1	36.9
Chironomid pupae	0.5	-	0.3
Unid. dipteran larvae	2.8	2.1	2.4
Odonata : Anisoptera nymphs	1.0	2.7	1.9
Ephemeroptera nymphs	0.2	-	0.1
Trichoptera larvae	3.5	8.9	6.2
Crustacea : Ostracoda	3.0	-	1.5
Arachnida : Hydracarina	4.9	0.7	2.8
Nematoda (free living)	5.7	0.7	3.2
Rhizopoda : Testaceae - *Difflugia*	1.8	0.7	1.2
Arcella	0.2	-	0.1
Allochthonous invertebrates			
Hymenoptera : Formicidae imagines	0.4	-	0.2
Lepidoptera larvae	0.2	-	0.1
Diplopoda : Polydesmida	0.2	-	0.1
Zooplankton			
Crustacea : Cyclopoid copepods	3.2	-	1.6
Claclocera - *Bosmina*	0.9	-	0.4
Rotifera - *Keratella*	0.7	-	0.4
Macrophyte material			
Leaf fragments	0.2	-	0.1
Seeds	0.5	-	0.3
Miscellaneous invertebrates	0.9	1.4	1.1
Mud/Sand	11.7	4.8	8.2

activity. Colonial algae, seeds and polydesmid millipedes were not consumed by the SSG while ephemeropteran nymphs, *Arcella*, leaf fragments, miscellaneous invertebrates and lepidopteran larvae were absent from the diet of the LSG. The IFP of algae, detritus, macrophyte material and zooplankton increased with fish size whilst that of benthic invertebrates, allochthonous invertebrates and mud/sand decreased ; there was no significant size-based variation in diet breadth (H' = 0.717 - SSG ; H' = 0.707 - LSG) ; this is reflected in the high dietary overlap (S = 75.9 %) between the size-guilds thus, indicating that the observed size-based differential exploitation of food resources was only to a slight extent.

Dietary shifts with maturity may result from changes in food predilection and/or foraging ability for the preferred dietaries. The ecological significance of diversification in fish diet with growth is that it reduces intraspecific competition and offers a wider spectrum of food resources for exploitation by the species (Whyte, 1975 ; Jacob and Nair, 1982).

Seasonal variation : The seasonality in the dietaries of *B. brachyistius* (Fig. 2) shows that the dry season food-richness (N_f = 25) was slightly higher than the wet season value (N_f = 21) ; these positively correlate with the seasonality in MFI (Fig. 3), thus corroborating the earlier assertion that food-richness increases with feeding intensity. This result is in consonance with Marcus' (1986) finding that

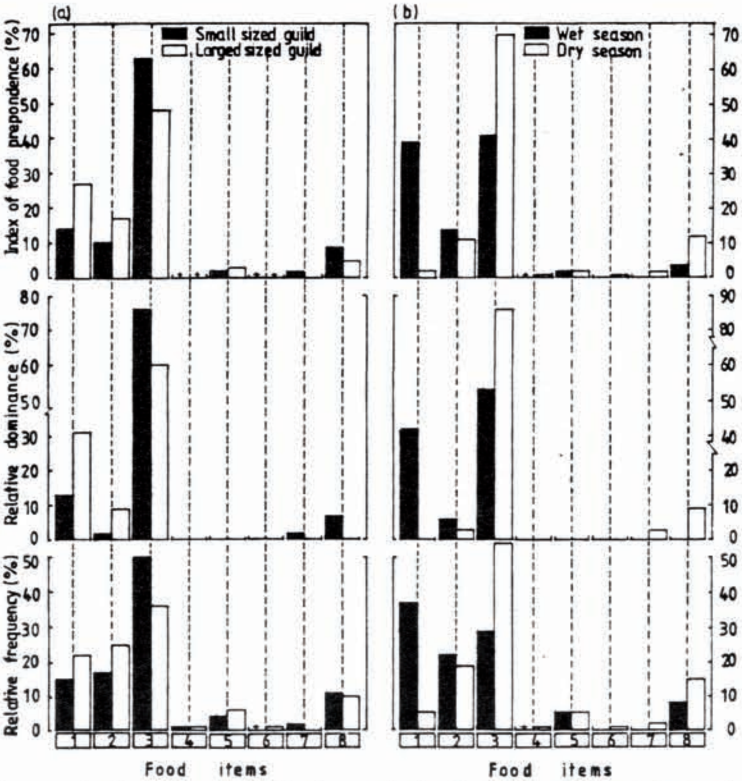

Fig. 2 : Ontogenetic (a) and seasonal (b) changes in the food composition of *B. brachyistius*. 1 : Algae ; 2 : Detritus ; 3 : Benthic invertebrates ; 4 : Allochtonous invertebrates ; 5 : Zooplankton ; 6 : Macrophyte materials ; 7 : Miscellaneous invertebrates ; 8 : Mud/sand. + : < 0.5 %.

Ilisha africana (Bloch) off the Lagos coast, Nigeria, feeds on a wider variety of items in the dry season but contradicts the reports of Lowe-McConnell (1964), Roberts (1972) and Welcomme (1979, 1985) that many tropical freswater fishes have a broader trophic spectrum during the rains (flood season).

Colonial algae, euglenids and polydesmid millipedes were not consumed during the dry season while ephemeropteran nymphs, *Arcella*, formicids, lepidopteran larvae and macrophyte material were not ingested in the wet season. Stout (1982) has reported a reduction in invertebrate abundances in tropical streams resulting from the impact of scouring discharge and Hynes (1975) has cited studies showing that the down-stream drift of invertebrates in rivers positively correlate with flow rate while Welcomme (1979) reviewed works suggesting wider dispersion and higher rate of dislodgement and downstream transport of benthic organisms during floods. Reduction in the abundance and availability of benthic invertebrates in Ikpa River by one or all the above methods, probably accounts for the decline in their importance (IFP) from 69.7 % in the dry season to 41 % during the wet season in *B. brachyistius* (Fig. 2). The fish then reverts to aufwuchs algae (particularly the filamentous forms) as a readily available alternative dietary ; the IFP of algae thus increased from 2.2 % in the dry season to 39.1 % in the wet season. Welcomme (1975) has reported of a substantial wet-season increase in the abundance of aufwuchs algae in some tropical rivers. The slight wet-season increase in the dietary importance of detritus (Fig. 2) is attributable to increase in allochthonous input of coarse particulate organic matter from the riparian zone through runoff as well as a decrease in abundance and availability of benthic invertebrates.

With the onset of the dry season and accompanying reduction in stream level and flow rate, the dietary importance of benthic invertebrates increased (Fig. 2)

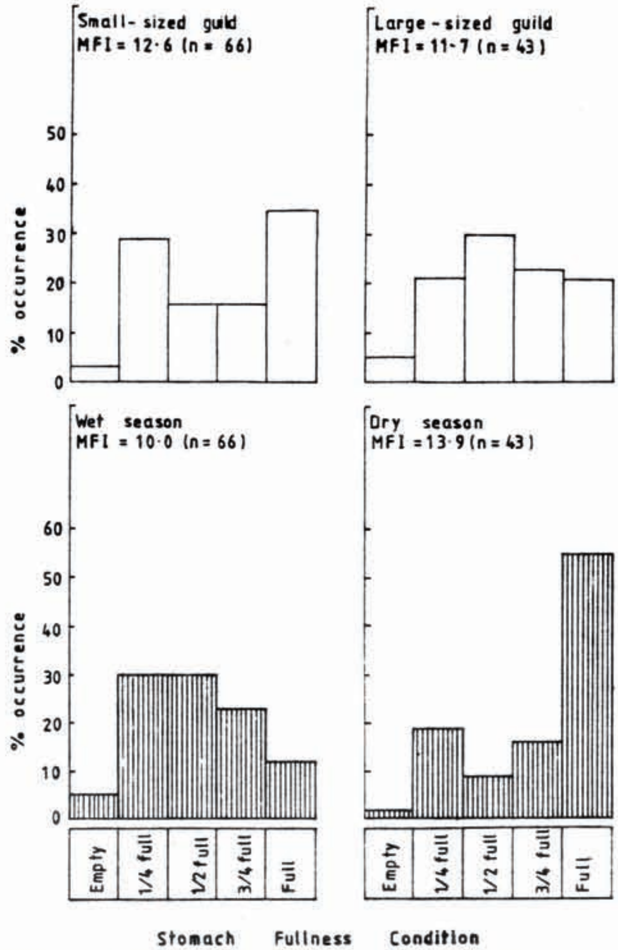

Fig. 3 : Ontogenetic and seasonal changes in stomach repletion and index of mean feeding intensity (MFI) of *B. brachyistius*.

perhaps as a consequence of greater abundance and availability ; this increase in the dietary preponderance of benthic invertebrate is reflected in the increase in the importance of mud/sand and the reduction in that of aufwuchs algae and detritus. The seasonality in food composition of *B. brachyistius* is further demonstrated by the moderate overlap value (S = 57.9 %).

The seasonal regime in diet breadth (dry season : H' = 0.692 ; wet season : H' = 0.796) revealed a slightly higher value during the rains. The optimal foraging theory (Schoener, 1971 ; Pyke *et al.*, 1977 ; Angermeier, 1982) postulates an inverse relationship between diet breadth and resource abundances ; this implies that diet breadth increases during periods of depressed resource abundances and declines during periods of high resource abundances. Assuming lower wet-season abundance of the most important dietary (benthic invertebrates) of *B. brachyistius* as already indicated, the higher H' recorded during this season conforms to the optimal foraging theory.

Functional morphology of alimentary tract :

B. brachyistius has a ventro-terminal mouth with non-protrusible premaxillae which are adapted for feeding largely on semi-sedentary benthic invertebrates as well as for browsing aufwuchs algae with the aid of the minute bicuspid premaxillary teeth. The mouth orientation is not well adapted for the ingestion of allochthonous invertebrates (e.g. formicids) some of which were apparently ingested at the air-water interface. The small mouth gape (2.3 - 3.3 % TL) of *B. brachyistius* tends to limit the prey size consumed ; this may explain the predominance of minute invertebrate prey in its diet (Table I) despite the presence of an enormous assemblage of large hydrophillid coleopterans, hemipterans and decapod crustaceans which are probably above the size threshold for attack by the fish.

The intestine, with a nearly uniform diameter, has a short relative length, ranging between 17.4 and 54.1 % TL (mean = 39.8 % TL) for specimens measuring 6.0 - 14.9 cm TL. The RIL and TL were inversely correlated ($r = -0.433$, $P < 0.01$, $n = 40$) ; an exponential regression of the form $\text{Ln (RIL)} = 4.114 - 0.0463\ \text{TL}$ accounted for only 18.7 % of the variation (r^2) in RIL.

The relatively short intestine of *B. brachyistius* is probably adapted to its diet of minute invertebrates but does not correlate with the large amount of algae and detritus also consumed ; the negative relationship between RIL and TL is also the reverse of the pattern of change in the relative importance of these dietaries with growth (Fig. 2).

Knöppel (1970), in a study of the food habits of fishes in Amazonian rainforest streams inferred *inter alia*, that snout structure, dentition, gut morphology and intestinal ratio were unreliable indices of feeding habits. This assertion, although upheld by Welcomme (1979), is considered by Roberts (1972) as 'too sweeping'. The failure to evolve functional morphological attributes for absolute trophic specialization as observed for *B. brachyistius* probably facilitates the evolution of diverse feeding habits and the ability to exploit different trophic niches.

Dynamics in feeding intensity

Variation with size : Figure 3 depicts the size-based changes in stomach repletion and MFI. Full stomachs dominated in the SSG and was closely followed by 1/4 full stomachs while 1/2 full stomachs predominated in the LSG ; MFI was slightly higher in the SSG. These indicate that feeding activity is higher in the SSG than in the LSG. Changes in feeding intensity with growth is an aspect of trophic niche partitioning which minimizes intraspecific competition (Jacob and Nair, 1982) particularly when different size-guilds exploit the same food resource base.

Diet variation : All specimens (6-13 cm TL, n = 48) from day catches had empty stomachs whereas only 4 (3.7 %) of 109 specimens (4-15 cm TL) from night catches had empty stomachs and 105 (96.3 %) contained food in fullness condition varying from 1/2 full to full. These reveal a high nocturnal feeding activity which declines during the day. This nocturnal foraging probably accounts for its being most abundantly caught at night.

Most of the benthic invertebrates that collectively constitute a substantial proportion of the diet of *B. brachyistius* (Table I) exhibit high nocturnal activity (see Hynes, 1975), hence the feeding periodicity of this fish is perhaps an adaptive response to the activity pattern of its prey. Roberts (1972) has noted that the nocturnal feeding behaviour of mormyrids correspond with the period of high susceptibility of benthic prey to predation ; their electrogenic and electrosensory organs enhance nocturnal foraging by enabling them to locate benthic prey electrosensorily while their weak electric emissions influence the prey in a manner that increases their susceptibility to predation. Another adaptive significance of the nocturnal feeding of *B. brachyistius* is that it lessens its vulnerability to predation by day-active piscine predators.

Seasonal variation : The seasonality in stomach repletion and index of mean feeding intensity (Fig. 3) indicate that 1/4 full and 1/2 full stomachs dominated during the rains while full stomachs predominated in the dry season ; MFI was higher in the dry season. These indicate a higher feeding intensity during the dry season, a pattern analogous to that of *Labeo fimbriatus* (Bloch) in an Indian river, in which case the reduced feeding activity during the rains was attributed to the washing away of its food by high current (Bhatnagar and Karamchandani, 1970). Reduction in abundance of benthic invertebrates (the most important dietary of *B. brachyistius*) (Table I) in Ikpa River during the rainy season as already opined (see seasonal variation in diet) may be responsible for the depressed feeding intensity of the fish. Moreover, since *B. brachyistius* has a penchant for shallow and slow-flowing water, it becomes more restricted in habitat preference during the rains by moving to increasingly sheltered positions to evade the increased stream level and flow ; this may result in the fish having limited accessibility to food resources with concurrent decline in feeding intensity. However, in the dry season, the decrease in stream level and flow are accompanied by widespread distribution of the fish which increases its accessibility to food resources with concomitant higher feeding intensity.

The seasonality in feeding regime of *B. brachyistius* in Ikpa River contradicts the trend in many tropical rivers where feeding intensity peaks during the rains (high water period) and declines in the dry season (slack water period) (Lowe-McConnell, 1964 ; Roberts, 1972 ; Welcomme, 1975, 1979, 1985, 1986).

CONCLUSION

This study reveals that the seasonality in rainfall, stream level and flow rate are important hydrometeorological factors that influence the food and feeding habits of *B. brachyistius* while the day-night cycle has some impact on its feeding periodicity and food preference. High water level and flow rate tend to limit its distribution to shallow-sheltered areas with slow-flowing water and indirectly depress food variety and feeding intensity. Its nocturnal foraging coincides with the nocturnal activity pattern of its benthic invertebrate prey. The ability of *B. brachyistius* to adapt to fluctuations in these environmental variables probably accounts for its success as the most common and abundant mormyrid in catches from the upper and middle reaches of Ikpa River.

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